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A Preliminary Study of Marsupial Relationships as Indicated by the Precipitin Test

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(Text-figures 1-7)

I. Introduction

It is one of the several tasks of the Serological Museum at Rutgers University, New Brunswick, New Jersey, to apply immunological techniques to problems of systematics and evolution. Both the theory and the practice of so doing have been substantially developed at Rutgers University since 1925.

The underlying assumption is that organisms may be better classified with a knowledge of the antigenic behavior of their proteins than without such knowledge. This in no sense implies that serological data should be the sole criterion of classification, but rather seeks to give such data their just due in the over-all body of systematic information.

Among the groups of animals of which the sera have to date been compared by the photronreflectometer method (Boyden & DeFalco, 1943) are Mammalia (Boyden & Gemeroy, 1950), Aves (DeFalco, 1942), Pisces (Gemeroy, 1943), Crustacea (Leone, 1950), and Insecta (Leone, 1947). The writer undertook to extend the studies of mammalian proteins by applying this classical technique to the available marsupial sera. Not since the pioneer experiments of Nuttall (1904) has this group figured in comparative serology.

II. Materials and Methods

The Antigens

The following marsupials figure in the tests described below:

Didelphis virginiana
North American opossum
Didelphoidea

Macropus rufus
Giant red kangaroo
Phalangeroidea

Macropus giganteus
Gray kangaroo
Phalangeroidea

Phascolomys ursinus
Wombat
Phalangeroidea

Sarcophilus harrisi
Tasmanian devil
Dasyuroidea

Perameles nasuta
Bandicoot
Perameloidea

With the exception of that of the opossum, the sera were obtained from bleedings done outside the United States. Preserved in merthiolate, all samples were kept at refrigerator temperature after arrival at the Serological Museum.

Preparation of Antisera

As is usual in systematic studies, the rabbit was the antiserum producer. 1 cc of 1:4 dilution of whole antigen in physiological saline was precipitated by 9 cc of 2% potassium alum at room temperature and .75 cc of the resulting mixture was injected intravenously into the rabbit's ear before any actual flocculation of serum protein could be observed. Beginning three weeks after the initial sensitization, four 1 cc amounts of the alum-precipitated antigen were injected subcutaneously at 48-hour intervals. Seven days after the final injection, a trial bleeding was made and the rabbit's serum tested for antibodies. If the reaction over several doubling

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dilutions of homologous antigen (1:500: 1:-4000) was of insufficient strength, a second series of four or five 1 cc quantities of undiluted, untreated antigen injected at 48-hour intervals was given, the first two doses being subcutaneous and the remainder intravenous. As before, a trial bleeding followed one week after the final injection.

If the antibody level was adequate, the rabbit was, within 24 hours, bled out by cardiac puncture. After separation from the clot by centrifugation, the antiserum was passed through a Seitz filter and bottled sterile at refrigerator temperature.

Powerful antisera to the first four antigens on the list were successfully obtained by this procedure. However, on three occasions individuals so treated with Tasmanian devil serum went into fatal anaphylactic shock during the booster series. The relatively weak but satisfactory antiserum finally developed resulted from an intravenous injection of 2 cc of untreated antigen followed two weeks later by three subcutaneous injections of 1 cc at 48-rour intervals. The very small quantity of bandicoot serum available made impossible any immunizing series with this antigen.

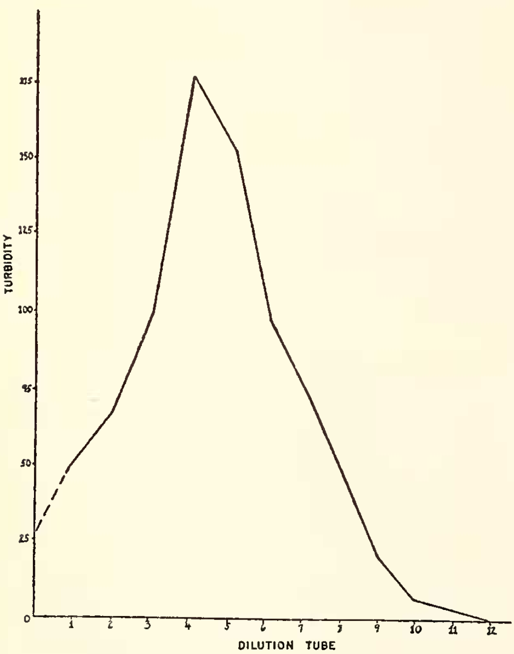
The Test

The amount of reaction between antigen and antibody (precipitin reaction) was determined by the use of the Libby photron'er as outlined by Boyden & DeFalco (1943). The full curve with its prozone, zone of optimal proportions and postzone was determined for a constant amount and concentration of antiserum. The total turbidity as defined by this curve was then obtained by adding all the individual turbidities of the cells in the test. Assigning the homologous total a value of 100%, the heterologous values were expressed as percentages of these homologous totals.

III. Results

Series 1

The anti-opossum serum used against the homologous antigen gives a total turbidity of 876 units with the peak at 180. Despite this considerable strength, all heterologous tests are negative.



Text-fig. 1. Opossum × anti-opossum.

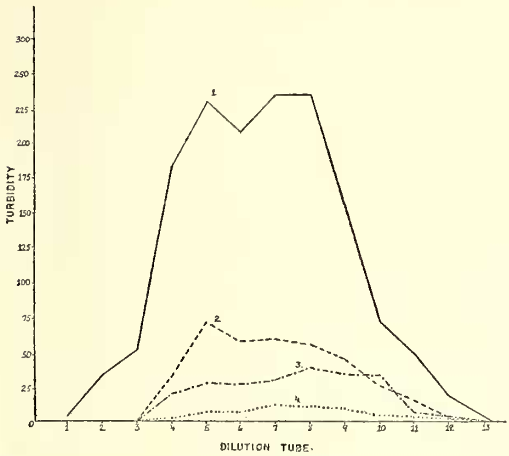
Table I. Antiserum to Didelphis virginiana (Opossum)

Antigen	Peak Turbidity	Total Turbidity	% Homologous
1. *Didelphis virginiana* (opossum)	178	876	100
2. *Macropus giganteus* (gray kangaroo)	N*	N	N
3. *Macropus rufus* (red kangaroo)	N	N	N
4. *Phascolomys ursinus* (wombat)	N	N	N
5. *Sarcophilus harrisi* (Tasmanian devil)	N	N	N
6. *Perameles nasuta* (bandicoot)	N	N	N

* N = No significant reading.

Series 2

The most powerful antiserum used in these determinations was that to the wombat. The curve seen in Text-fig. 2 is typical of one obtained when the source of the antibody is a rabbit repeatedly injected over an extended period of time, and the four dilution spread of the zone of optimal proportions is indicative of a relatively low antiserum specificity. The peak value (234) is very high, as is the total turbidity. The heterologous values in percent of the homologous total are: red kangaroo, 25%; gray kangaroo, 16%; and Tasmanian devil, 5%. Neither the opossum nor the bandicoot antigens react.



Text-fig. 2. Wombat × anti-wombat.

Series 3

Anti-gray kangaroo serum, although not of excessive strength, reacts with three out of five heterologous marsupial antigens as follows: to 64% of the homologous total with red kangaroo serum, to 17% of the homologous total with wombat serum and to 7% with Tasmanian devil serum. Opossum and bandicoot sera do not react with this antiserum.

Text-fig. 3. Gray kangaroo × anti-gray kangaroo.

Table II. Antiserum to Phascolomys ursinus (Wombat)

Antigen	Peak Turbidity	Total Turbidity	% Homologous
1. *Phascolomys ursinus* (wombat)	234	1505	100
2. *Macropus rufus* (red kangaroo)	70	371	25
3. *Macropus giganteus* (gray kangaroo)	43	240	16
4. *Sarcophilus harrisi* (Tasmanian devil)	16	83	5
5. *Didelphis virginiana* (opossum)	N*	0	0
6. *Perameles nasuta* (bandicoot)	N	0	0

* N = No significant reading.

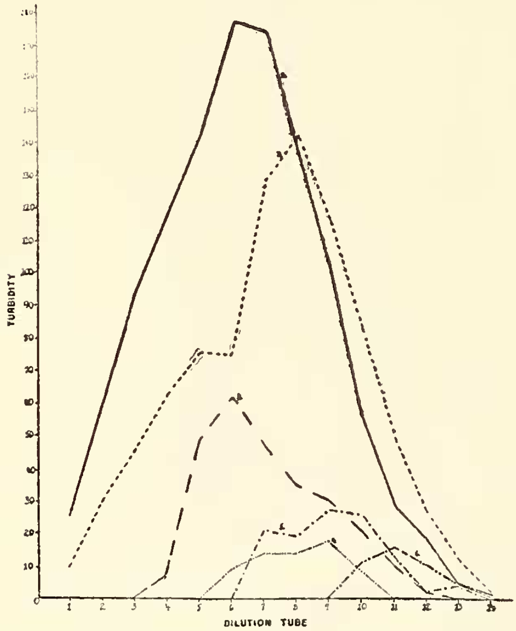
Table III. Antiserum to Macropus giganteus (Gray Kangaroo)

Antigen	Peak Turbidity	Total Turbidity	% Homologous
1. *Macropus giganteus* (gray kangaroo)	124	604	100
2. *Macropus rufus* (red kangaroo)	93	355	64
3. *Phascolomys ursinus* (wombat)	31	105	17
4. *Sarcophilus harrisi* (Tasmanian devil)	14	46	7
5. *Didelphis virginiana* (opossum)	N*	0	0
6. *Perameles nasuta* (bandicoot)	N	0	0

* N = No significant reading.

Series 4

The powerful antiserum made to the red kangaroo antigen is the only one to react with opossum and bandicoot antigens. The value is 10% of the homologous one in the first case and 4% in the second case. The other three heterologous values are: 80% with gray kangaroo serum, 24% with wombat serum and 4.5% with Tasmanian devil serum.



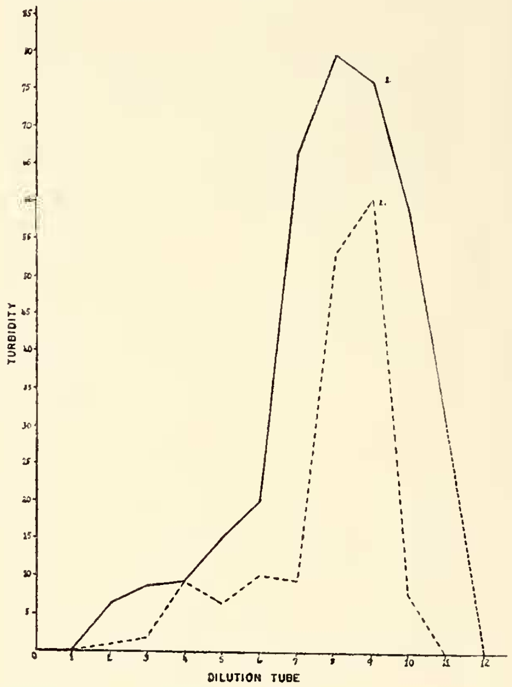
Text-fig. 4. Red kangaroo × anti-red kangaroo.

Table IV. Antiserum to Macropus rufus (Red Kangaroo)

Antigen	Peak Turbidity	Total Turbidity	% Homologous
1. *Macropus rufus* (red kangaroo)	177	1148	100
2. *Macropus giganteus* (gray kangaroo)	142	921	80
3. *Phascolomys ursinus* (wombat)	62	286	24
4. *Sarcophilus harrisi* (Tasmanian devil)	18	54	4.5
5. *Didelphis virginiana* (opossum)	27	114	10
6. *Perameles nasuta* (bandicoot)	15	43	4

Series 5

Made to the Tasmanian devil, this antiserum, the weakest of the five, reacts only with the wombat among the heterologous antigens. The total is 42% of the homologous.



Text-fig. 5. Tasmanian devil × anti-Tasmanian devil.

Table V. Antiserum to Sarcophilus harrisi (Tasmanian Devil)

Antigen	Peak Turbidity	Total Turbidity	% Homologous
1. *Sarcophilus harrisi* (Tasmanian devil)	79	367	100
2. *Phascolomys ursinus* (wombat)	60	157	42
3. *Macropus rufus* (red kangaroo)	N*	0	0
4. *Macropus giganteus* (gray kangaroo)	N	0	0
5. *Didelphis virginiana* (opossum)	N	0	0
6. *Perameles nasuta* (bandicoot)	N	0	0

* N = No significant reading.

IV. Discussion.

Simpson (1945) gives the following systematic interpretation of the Order Marsupialia. There is general agreement that it reflects the natural relationships as evident from structural comparisons and fossil history.

1. The Didelphoidea are the primitive marsupial stock with several persisting lines, among them the New World opossums.

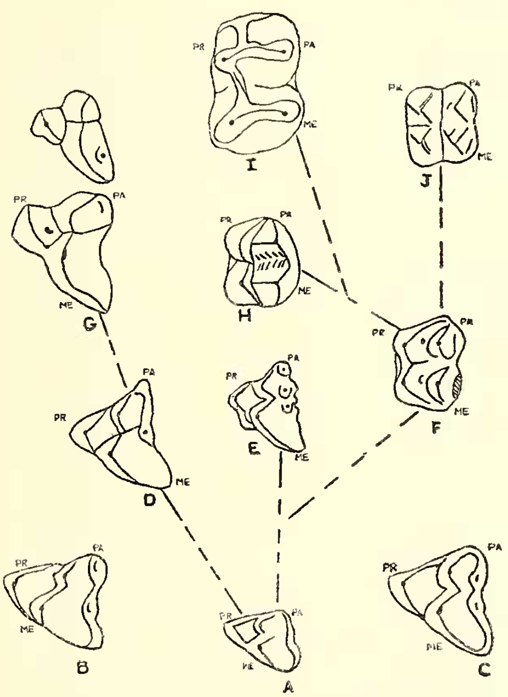
2. Five other groups arose from primitive didelphoid types.

3. If any two of them have a common ancestry, it was for a very brief period and at a remote time.

4. All five arose at about the same time and have since been entirely distinct.

The six groups are assigned the rank of superfamily:

1. Didelphoidea	opossums
2. Dasyuroidea	native "cats"
3. Borhyaenoidea	......
4. Perameloidea	bandicoots
5. Caenolestoidea	marsupial "rats"
6. Phalangeroidea	kangaroos, wombats



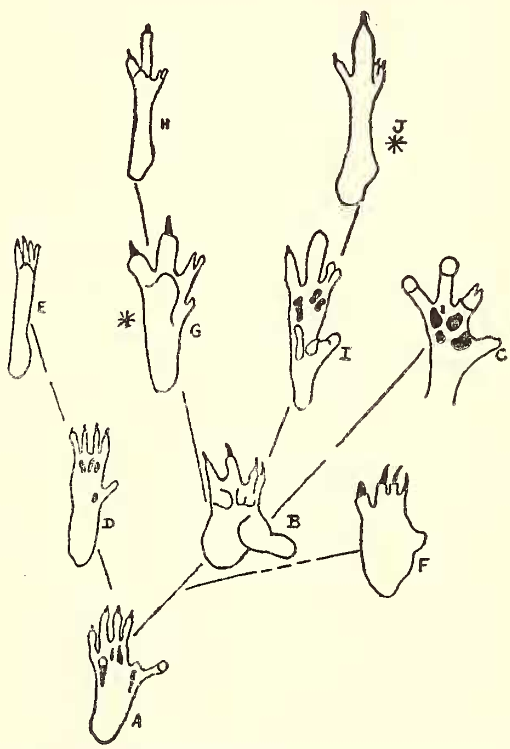
Text-fig. 6. Patterns of upper molar teeth in marsupials, and their probable phylogeny. A—*Peratherium fugax*. B and C—*Didelphys virginiana*. D—*Dasyurus viverrinus*. E—*Perameles nasuta*. F—*Petauroides volans*. G—*Thylacinus cynocephalus*. H—*Trichosurus vulpecula*. I—*Macropus* sp. J—*Phascolarctos cinereus*. PR—Protocone. PA—Paracone. ME—Metacone. (*After* Bensley, 1901, The American Naturalist, 35: 245-269).

Of these, the Borhyaenoidea, large South American carnivorous marsupials, are extinct.

These superfamilies represent general adaptive types, evolved during the radiation of the order. The contemporary situation is illustrated by Text-figs. 6 and 7. Text-fig. 6 shows the types of upper molar teeth found in the various marsupial families. A is that of an extinct didelphid, *Prototherium fugax,* while B and C are two representative species of contemporary opossums, *Didelphis azarae* and *Didelphis virginiana.* The dotted lines indicate the postulated evolution from the basic type.

As is the case with the teeth of placental mammals, there are omnivorous, carnivorous and herbivorous types, the first represented by the Didelphoidea and Perameloidea (E), the second by the Dasyuroidea (D and G), and the third by the Phalangeroidea (I and J). In general, the parallelisms with the molars of placentals in similar ecologic niches are quite evident.

Text-fig. 7 shows the various types of pes to



Text-fig. 7. Modifications of the pes in marsupials, and their probable phylogeny. A—*Didelphys nudicaudata*. B—*Phalanger celedensis*. C—*Tarsipes rostratus*. D—*Sminthopsis murina*. E—*Antichinomys laniger*. F—*Phascolomys latifrons*. G—*Perameles doreyana*. H—*Peragale leucura*. I—*Hypsiprymnodon moschatus*. J—*Macropus* sp. (*After* Dollo, in Bensley, 1901, The American Naturalist, 35: 245-269).

be found in the order. A is an arboreal appendage typical of the opossums. D and E are dasyurid modifications; G and H are perameloid modifications; and the remaining ones are various phalangeroid modifications.

There are two criteria for the formation of supergroups of the marsupial subdivisions: dentition and foot pattern. The former distinguishes the Diprotodontia (two incisor teeth) and the Polyprotodontia (many incisor teeth). Thus:

Polyprotondontia	
Didelphoidea	opossums
Borhyaenoidea	....
Dasyuroidea	Tasmanian devil, etc.
Perameloidea	bandicoots
Diprotodontia	
Caenolestoidea	marsupial "rats"
Phalangeroidea	kangaroos, wombats, etc.

The second distinguishes the Didactyla (second and third digits separate) and the Syndactyla (second and third digits fused). Thus:

Didelphoidea	
Didelphoidea	opossums
Borhyaenoidea	....
Dasyuroidea	Tasmanian devil, native "cats" etc.
Caenolestoidea	marsupial "rats"
Syndactyla	
Perameloidea	bandicoots
Phalangeroidea	kangaroos, wombats, etc.

There are two anomalous groups, the bandicoots, which are polyprotodont and syndactylous, and the marsupial "rats," which are diprotodont and didactylous. Of the other four, all those which are polyprotodont are didactylous and all those which are diprotodont are syndactylous. The basis for the intra-ordinal classification of the marsupials is thus very similar to that for the classification of placental mammals at both the ordinal and the family levels, for digit pattern and dentition are certainly the most common criteria applied by the mammalian systematist.

How may the results of the precipitin tests be integrated with the morphological picture outlined above? Perhaps the best procedure is to discuss each antiserum individually, interpreting each reaction series as if it were the only one available, and then attempting integration.

Series 1. Anti-opossum serum

On the basis of morphology, the Didelphoidea have been considered as being remote from the other superfamilies of the order, and the serological evidence obtained from this series of tests confirms such a view. The strength of the antiserum employed is sufficient to enable slight but significant heterologous reactions to occur were there any ordinary similarities in the nature of the homologous antigen and any heterologous antigen. It is essential to remember, however, that the source of antigen was a contemporary opossum, as far removed in time from the ancestral didelphid as are the animals from which the various heterologous antigens were taken. Conservative a trait as serum protein structure is reputed to be, sufficient changes to distinguish the proteins of the present opossum quite markedly from those of the didelphid common ancestor may have occurred. One of the major limitations of serological systematics is the impossibility of evaluating the proteins of extinct forms.

Series 2. Anti-wombat serum

The great power of this antiserum makes the results extremely important, for a high turbidity peak and a broad zone of optimal proportions indicate an antibody complex of low specificity which should respond to even slight similarities in heterologous sera.

As would be expected, the other phalangeroid sera (those of the red and gray kangaroos) yield the strongest heterologous tests. More surprising is the reaction with the Tasmanian devil antigen in the complete absence of any reaction with the anatomical intermediates, bandicoot and opossum. On the basis of a serological comparison alone, the Tasmanian devil is more similar to the wombat than to the type most resembling the presumptive ancestor. The relationships of the bandicoot and opossum to the wombat must be quite remote, since even an antiserum with such power and low specificity failed to react with either one.

Series 3. Anti-gray kangaroo serum

The gray kangaroo antiserum behaves in a manner similar to the anti-wombat serum in that the morphological intermediates show no reaction while a slight but definite turbidity curve develops when the Tasmanian devil antigen is tested. In this case also, the greatest serological correspondence coincides with the anatomical similarities, since a companion species of the same genus (red kangaroo) has the greatest heterologous turbidity and a member of the same superfamily (wombat) has the second greatest.

Series 4. Anti-red kangaroo serum

The reactions of the red kangaroo antiserum reflect the classic morphological interpretation of marsupial relationships. On the basis of these curves alone, the conclusion would be that current serological differences among the families correspond exactly to the proposed phylogeny. There seems to be no doubt about the validity of the opossum curve. A heterologous value of 10% is significant, and a typical progression through a peak of 27 establishes its conformity to the course of a precipitin reaction with antiserum constant and antigen variable. The test was run three times with comparable results in the other two cases. Although the Tasmanian devil and the bandicoot curves are barely within the margin of significance, the great power of the antiserum and again the typical curve pattern justify their acceptance as valid reactions.

Series 5. Anti-Tasmanian devil serum

It is unfortunate that a more powerful Tasmanian devil antiserum was not obtained. However, the results are not in any way contradictory. The only heterologous antigen which showed any reaction was the wombat serum. The reciprocal of this test (Tasmanian devil and anti-wombat) yielded higher turbidities than any other heterologous test involving the same antigen. Additional confirmation may be found in the considerable serological differences obtained between the two species of the genus *Macropus* on one hand and the wombat on the other. In other words, the negative results of the kangaroo tests may be accounted for by regarding the antigen factors held in common by them and the Tasmanian devil to be different from those held in common by the wombat and the Tasmanian devil. The actual quantitative result is open to question. Were the antiserum more powerful, the 42% heterologous total should be markedly reduced due to an increase in the homologous turbidity.

Integration of these preliminary data raises several points, one pertaining to the nature of the tests and the others to relationships among the organisms tested. The conjectural nature of the latter group is, of course, a function of the small number of marsupial antigens available in the Serological Museum at the present time. Until this collection is strengthened, marsupial systematics may be discussed only in the broad outline.

1. The evaluation of the small reactions must be given very careful consideration, since the quantitative expression of serological relationship as determined by the photron'er is definitely limited to reactions of reasonable strength. Numerical totals may vary considerably with different lots of antisera and antigen samples. What does remain constant at all levels is the order of the relation of heterologous antigens to the homologous antigen. When dealing with values under 10%, however, there is danger of a distorted result due to factors such as slight errors in timing, pipetting, etc., which have no significant effect on stronger reactions—such distortions are possible at all levels if the antiserum is weak. Thus, an apparent reversal of heterologous order might be observed in different determinations as a result of a summation of slight technical aberrations, and, in the same manner, a marked change in total value (say from 3% to 6%) might also be seen. It is, therefore, important to note the form of the curve so that the addition of small erratic increments does not give the impression of a precipitin reaction where none has actually taken place.

The curves representing the reactions figuring in these studies have been so examined and found to conform to the typical three zone pattern, and hence these reactions represent slight similarities between the serum proteins of the two animals in question in each test.

2. The intrafamilial systematics of the phalangeroids, as determined by comparative serology, confirms the morphological classification in all three series involving antisera to antigens of this group. Also, it may be said that wombat stands in closer relationship to red kangaroo than to gray kangaroo. Both anti-wombat serum and anti-red kangaroo serum in respective heterologous tests reveal a correspondence of about 25% between the antigens involved, while both anti-wombat and anti-gray kangaroo serum in respective heterologous tests reveal a relationship of about 17% between the antigens involved.

3. Biochemical differences among the various marsupials do not seem to be in the same pattern as the morphological differences. Heterologous reactions reveal a greater similarity among anatomical extremes than between either extreme and the morphological intermediates (opossums and bandicoots). That the serum of the Tasmanian devil, a dasyurid, should react with antisera made to phalangeroids like the wombat and the kangaroo in the complete absence of any reaction with anti-opossum serum indicates a need for a thorough re-examination of the systematics of this order. The similarity of the extremes is confirmed by the fact that the anti-Tasmanian devil serum bridges the morphological gulf reciprocally to react with the wombat antigen and only the wombat antigen.

4. The isolation of the opossum and the bandicoot is very striking, particularly since these forms have no similarity to each other, if the result of the bandicoot anti-opossum test is any criterion.

5. Most interesting are the reactions between the antiserum formed to the red kangaroo and

the opossum and bandicoot antigens respectively. In the complete absence of any complementary evidence from the reciprocal test with anti-opossum serum or of any reaction between either antigen and the antiserum to the gray kangaroo, an animal in the same genus as the red kangaroo, it seems unlikely that these results reflect a systematic relationship. Nor is convergent biochemical evolution a promising explanation. In the first place, it would be unique in the data of serological comparison; and, secondly, the reciprocal test should be positive just as in the case of a true systematic relationship. The writer is most inclined to the view that the antiserum contains some anomalous substance not typical of rabbits in general, capable of a heterophilic reaction with opossum and bandicoot sera. In any case, no conclusions may be drawn until other tests are possible as well as a repetition of the anti-red kangaroo series.

6. It is illuminating to relate the serological data from these tests to the so-called "serological yardstick" of Boyden (1943), who states: "To date, the photron'er has been or is being applied to the study of [Insecta, Pisces, Aves, Crustacea and Mammalia]. Essentially the same types of results have been obtained in all these groups and no one by looking at a series of curves could tell from which animals the curves were derived . . . the amounts of serological divergence run, in general, in accordance with the rank of the systematic category . . ."

He then lists the magnitude of correspondence usually found among members of the same genus, among different genera in the same family and among different families. There is such a surprising consistency among widely different systematic groups that Boyden believes it possible to utilize these values as abstract standards of systematic rank and, thus, to resolve the eternal "conflict between 'lumpers and splitters'." He notes, for example, that antisera made to birds will react with all orders of birds and hence concludes that avian orders are the equivalent of the more distantly related mammalian families.

Applying this line of reasoning to the Order Marsupialia, we find mixed results. The high correspondence within the genus *Macropus* is quite in line with that in placental species of the same genus (60%+), yet the other member of the Superfamily Phalangeroidea represented in these data, the wombat, has a correspondence to the genus *Macropus* which is that of a rather distantly related family. By placental standards, one would expect an order of 40%-60% similarity in heterologous reactions between the two genera. The Dasyuroidea, represented by the Tasmanian devil, show the differences one would expect from widely divergent families with respect to the Superfamily Phalangeroidea. The Didelphoidea and Perameloidea, by the "serological yardstick," are of greater than familial distance from the Dasyuroidea and Phalangeroidea and, judging by the results of the bandicoot anti-opossum test alone, are at least as great a distance from each other.

7. The two sets of high level taxa which break up the order, by dentition on one hand (Polyprotodontia or Diprotodontia) and pes form on the other (Didactyla or Syndactyla), appear to have as little meaning in the light of the serological data as they have in reference to each other. To cite only one instance, it would be expected that anti-Tasmanian devil serum would react more readily with opossum serum that with wombat serum, since the phalangeroid wombat is separated from the dasyurid Tasmanian devil by both classifications. This is, of course, not the case.

The marsupials present problems in systematics which are more difficult than most. It has long been recognized that the group embraces more diverse types than any placental order and that a continuous spectrum between adaptive extremes is the rule rather than a series of sharp breaks. Such a situation always increases the difficulties of the taxonomist using a morphological approach. This complication is compounded by the fact that marsupials are overshadowed in the minds of zoologists by the eutherians and that the former are almost inevitably judged by the standards of the latter. Since its techniques minimize the subjective element and have, indeed, great claim to being quantitative in the true numerical sense of the word, comparative serology is admirably suited as a tool for the systematic study of such a controversial group. It is of particular importance that this study be pursued beyond the preliminary level represented by the data so far obtained, because these data indicate that the morphological interpretation of interfamilial relationships among marsupials may be a false one.

Let it be emphasized that the nature of the serum proteins is a very conservative trait which is frequently a truer indication of the relationship between two organisms than anatomical similarities. For example, no antiserum to a placental mammal would react with a marsupial antigen or vice versa, thus making such tests as valid a criterion for separation as the great differences in the reproductive systems. Certainly it is worth while to continue serological comparisons within the order and to see whither we are led. It is quite possible that, in addition to defining a new arrangement of marsupial types and determining the value of species and genera by the "serological yardstick," much may be learned about parallel and convergent evolution in structural or serological characters, or in both.

Summary

1. Several representative marsupial sera were compared, using the photron'er technique of Boyden (1943).

2. The results indicate that serological relationships among the various marsupial families may not correspond to the relationships postulated from dentition and pes form.

3. The only family represented by more than one species in these tests exhibits the expected intrafamilial similarities in the serum proteins.

4. Extrafamilial correspondence is slight in some cases and nonexistent in others. This confirms the opinion that the order contains more diverse groups of animals than do the placental orders.

5. The advantages of the serological approach in systematic problems of this nature are brought out.

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